Title: Long-term community change through multiple rapid transitions in a desert rodent community

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Abstract

While studies increasingly document long-term change in community composition, whether long-term change occurs gradually or via rapid reorganization events remains unclear. We used Latent Dirichlet Allocation (LDA) and a change-point model to examine the long-term dynamics of a desert rodent community undergoing compositional change over a 38-year span. Our approach detected three rapid reorganization events, where changes in the relative abundances of dominant and rare species occurred, and a separate period of increased variance in the structure of the community. These events coincided with time periods—possibly related to climate events—where the total abundance of rodents was extremely low. There are a variety of processes that could link low abundance events with a higher probability of rapid ecological transitions, including higher importance of stochastic processes (i.e., competitive interactions or priority effects) and the removal of structuring effects of competitive dominants or incumbent species. Continued study of the dynamics of community change will provide important information not only on the processes structuring communities, but will also provide guidance for forecasting how communities will undergo change in the future.

Key words: community dynamics, Latent Dirichlet Allocation, desert rodents, temporal dynamics, extreme climatic events

Introduction

As humans alter the template of nature by increasing temperature, changing nutrient distributions, and altering land cover (Walther 2010), the composition of species living in these places also changes. Compositional changes occur both directly as each species responds to the environment in the context of its own needs or preferences, and indirectly through changes in the competitive landscape and other species interactions. Depending on the mechanisms driving community change, this change can be gradual or rapid. Gradual change can occur through stochastic turnover events, or niche-based turnover as species' ability to thrive gradually improves or degrades as the environment changes (e.g. Tingley et al. 2009). Rapid changes in communities can emerge as ecosystems respond to intrinsic or extrinsic drivers (Williams et al. 2011). With intrinsically-driven rapid change, sometimes referred to as regime shifts, gradual changes in the environment eventually push the ecosystem past a threshold, triggering rapid shifts to an alternate stable state (Scheffer and Carpenter 2003). Extrinsically-driven rapid changes can occur either from niche-based tracking as the environment rapidly shifts from one state to another (Beaugrand 2004), or via extreme events, which cause cascading changes in species populations that alter how the community recovers post-disturbance (Smith 2011).

While a growing number of studies document the occurrence of rapid ecological transitions (Beaugrand 2004, Thibault and Brown 2008), meta-analyses compiling data from many long-term studies indicate that most communities are changing gradually over time (La Sorte and Boecklen 2005, Dornelas et al. 2014). This discrepancy may arise because studies focused on rapid ecological transitions are asking different questions than meta-analyses examining community change. Because these events are unpredictable and abrupt, studies of rapid ecological transitions typically focus on relatively short time-scales and include only the dynamics immediately before and after the specific event being studied (e.g. Thibault and Brown 2008). In contrast, meta-analyses of community change focus on the trends occurring over decades and may intentionally average out or avoid periods of rapid transition. Because studies of rapid ecological transitions and meta-analyses are focused on different patterns at different time scales, it is unknown whether rapid ecological transitions are truly rare events. Answering this question requires high frequency, long-term monitoring data and methods that are able to detect these dynamics in ecological time series.

Here, we examine community change through time in a desert rodent community. Surveyed monthly from 1977 to 2015, this rodent community has undergone significant turnover. Both rapid and gradual reorganization have been invoked to explain these changes in rodent composition. Using linear approaches typically used in meta-analyses and applied to annual or seasonal data, rodent species turnover was interpreted as indicative of gradual long-term response to habitat shifts from open arid grassland to shrubland (Ernest et al. 2008). Other studies, focused on the impacts of specific climate events on the rodent community, have proposed that these events triggered rapid shifts in community composition (Valone et al. 1995, Thibault and Brown 2008). Thus this is an ideal data set for assessing how to reconcile short-term events with long-term community change at the multi-decade scale.

Methods

To examine the dynamics of this community, we used 38 years of monthly rodent data from the Portal Project, a long-term study located on 20 hectares of Chihuahuan Desert near the town of Portal, Arizona, USA. This site has undergone considerable habitat change: a 3-fold increase in woody vegetation between 1977 and the mid-1990s transitioned this site from an open desertified grassland with widely scattered woody shrubs to a desert shrubland (Brown et al. 1997). Small mammal data is collected at this site on 24 permanent 50m by 50m plots, sampled at monthly intervals with no major changes in methodology since 1977. Here, we pool data from the 8 unmanipulated ("control") plots, which allow unrestricted access to all species from the regional pool, to provide one site-level estimate of the natural dynamics of the rodent community from 1977-2015. Data for our analysis consisted of a table of counts for each species for each month of the time series. This amounted to 436 time steps and 21 species.

The twenty-one rodent species caught at the site consist primarily of granivorous rodents, with some insectivorous or folivorous species. The body size range of this community spans from 6 grams to nearly 200 grams. This community has experienced considerable turnover in species composition through time, with only two species captured consistently at almost every survey since 1977. Further information on the site and protocol can be found in Brown (1998) and Ernest et al. (2016). The latter paper also contains the data used in this analysis.

To quantify the dynamics of species composition, we used a 2-step approach. First, we reduced the dimensionality of composition data (i.e. condensed the species-level information on presence/absence and abundances) using a method from machine learning (Latent Dirichlet Allocation; see Blei et al. 2003) that is capable of detecting subtle or abrupt changes in composition. We then quantified the dynamics of this simplified composition time series using a change-point model (Western and Kleykamp 2004). We demonstrate the 2-step approach with a set of simulated data in Appendix S1.

Identifying species associations using Latent Dirichlet Allocation

Latent Dirichlet Allocation (LDA) was developed as an alternative to cluster analysis for summarizing documents based on the words they contain. This machine learning approach was recently introduced to ecology as a way to quantify changes in species composition across gradients (see Valle et al. 2014). LDA takes the words in a document and identifies “topics” – collections of words that tend to be found together in specific proportions (Blei et al. 2003).

Whereas clustering approaches assign each sample (“document”) to exactly one cluster, LDA attempts to infer the relative contributions of all topics. If these contributions change gradually over time, then these changes in document composition can be tracked from sample to sample. When applied to ecological data, this technique can summarize community observations (“documents”) based on the species (“words”) they contain. Analogous to collections of words forming topics in document analysis, LDA identifies groups of species that tend to be found together in specific proportions. Rather than looking at raw species composition in a collection of community observations (for example over a gradient in space or time), LDA is able to: 1) reduce species composition at each sampling point to its community-type composition, and 2) describe each community-type in terms of the species it contains, which may reveal important information about underlying species associations.

Fitting an LDA model involves simultaneously determining two sets of numbers: one defining the community-types, and one describing the observed species assemblages in terms of those types. Due to the complex relationship between the way each community-type is defined and its influence on individual assemblages, exact inference is not possible in this model. We used Blei et al.’s variational approximation, which simplifies this relationship. This approximation allowed us to use Blei et al.’s (2003) iterative “variational expectation-maximization” procedure for jointly optimizing both sets of parameters, as implemented in the `topicmodels` package (version 0.2-7) (Hornik and Grün 2011) for R 3.3.2 (R Core Team 2016). Like many clustering and ordination methods, LDA requires the number of community-types to be specified as model input (it does not determine the number of community-types supported by the data). We used an approximate AIC procedure (based on a variational approximation to the full likelihood function) to inform the appropriate number of community-types needed to best describe the data (Appendix S2: Fig. S1). See Valle et al. 2014 for a thorough description of LDA in an ecological context, and comparison of LDA to traditional clustering techniques.

Quantifying when change occurs using a change-point model

LDA is a discovery tool which simplifies multivariate species composition to better visualize community dynamics. However, it does not tell us if (or when) a change in community structure has occurred. We fit a change-point model (Western and Kleykamp 2004) to identify abrupt transitions in the time series of community-types generated by the LDA model. Change-point models break up a time series into intervals, with a different set of parameters to describe the time series during each interval. Between each pair of change-points, we modeled each community-type's prevalence as a sinusoid with a period of one year, to control for seasonal fluctuations. The community-type proportions in each interval were modeled using a separate multinomial generalized linear model fit with the nnet package (Venables and Ripley 2002). Because we were modeling proportions rather than counts, this model gave us a *quasi*-likelihood for each interval, rather than a conventional likelihood (McCullagh and Nelder 1989). Since our quasi-likelihoods did not inflate the variance, however, they can be interpreted on the same scale as a conventional likelihood for purposes of model comparison (Anderson et al. 1994). The product of interval-level quasi-likelihoods yields the quasi-likelihood for the full data set; this value will be largest when the change-points break the time series into relatively stable intervals that can be explained well by the generalized linear model.

The number of possible change-point locations was too large to evaluate all the possibilities exhaustively, so we used Markov chain Monte Carlo (MCMC) to collect a representative sample of change-point locations that are consistent with the data. Initial experiments with Metropolis sampling showed poor mixing, so we implemented a parallel tempering sampler (also called Metropolis-coupled MCMC and replica-exchange MCMC) to facilitate movement of the Markov chain between modes via exchanges with auxiliary Markov chains that rapidly explore the space of possible change-points (Earl and Deem 2005). We fit change-point models with up to five change-points for the rodent data, and evaluated model performance by comparing the average log-quasi-likelihood to the number of model parameters (Gelman et al. 2014).

Results

Rodent species composition over the 40 years of the study was best described using four different community-types (Appendix S2: Fig. S1, Table S1). Our four community-types share some species (though they differ in relative abundances), while other species are unique to one or two community-types (Fig. 1a). Our four community-types differ in which species are the most abundant. The most abundant members of community-types 1 and 2 are kangaroo rats from the genus *Dipodomys*: community-type 1 is co-dominated by *D. spectabilis* and *D. merriami*, while community-type 2 is dominated by *D. merriami* alone. In contrast, the most abundant members of community-types 3 and 4 are pocket mice from the genus *Chaetodipus*: community-type 3 is dominated by *C. baileyi* and community-type 4 by *C. penicillatus*. In Fig. 1a, the 21 species are arranged on the x-axes in order of decreasing body size and grassland-affiliated species are denoted with bold outlines on their bars, to demonstrate that the four community-types differ not only in the identity of species making up the community, but also the distribution of body sizes (Ernest 2013) and habitat preferences contained in the community.

Through time, the different community-types varied in their prevalence and dynamics

(Fig. 1b). When the study began, the desert rodent community mainly consisted of community-type 1 (Fig. 1, light blue). In the mid-1980s, the rodent community transitioned to community-type 2 (Fig. 1, dark blue) and then transitioned again in the late 1990s to become a mix of community-types 2, 3, and 4 (Fig. 1, dark blue, gold, and grey, respectively). Finally, around 2010, the community entered its current state which is seasonal oscillations between community-types 2 and 4 (Fig. 1, dark blue and grey). These dynamics and community-types are consistent with previous studies that documented the decline of *D. spectabilis* (the co-dominant species of community-type 1) in the mid-1980s (Valone et al. 1995), the colonization and rise to dominance of *C. baileyi* (the dominant species in community-type 3) in the late-1990s (Ernest and Brown 2001), shifts in the body size structure of the community from large species to smaller species (White et al. 2004), and a general decline in grassland-affiliated species and an increase in shrubland-affiliated species (Ernest et al. 2008).

Visually, the LDA results suggest that major shifts in community dynamics occurred multiple times over the study. Using our change-point approach, we found that a model containing four change-points was best supported by the data (for comparison of models containing 2, 3, 4, and 5 change-points see Appendix S2: Fig. S2). Histograms showing the locations of these four change-points are shown in Fig. 2c, with the distribution of each point shown in a different shade of gray. Using these distributions, we located the 95% credible interval for when each of these transitions occurred: December 1983-July 1984, October 1988-January 1996, September 1998-December 1999, and June 2009-September 2010. Fig. 1d shows the change-point model's estimate of how the prevalence of the four community-types differs before and after each transition event, demonstrating that three of these events (1984, 1998-1999, 2009-2010) are driven by a shift in which community-type is most prevalent, marking a major shift in community structure.

The 1988-1996 transition differs from the other three major reorganization events. It has a broader change-point distribution, and there is no change in which community-type is dominant. However, this change-point indicates an increase in the variance (amplitude) of the dominant community-type through this period. Minor changes in community structure also occur as community-type 1 disappears and community-types 3 and 4 increase in prevalence. Together these dynamics suggest the 1988-1996 transition is not a rapid shift in community structure like the other events, but is instead either an increase in the variance of community structure and/or a signal of a very slow shift in species composition that was abruptly terminated with the major reorganization event of 1998-1999. We also repeated analyses with three, five and six community-types in case our results were highly sensitive to the number of community-types specified, and qualitatively, the results we discuss are generally robust (see Appendix S2: Fig. S3, Fig. S4, Fig. S5 for comparison).

Discussion

Over nearly 40 years, the rodent community at the Portal Project has changed substantively, with shifts in species composition, dominance structure, and distributions of body sizes and habitat affiliations (Fig. 1). Our results are consistent with earlier studies which described the replacement of grassland-affiliated species by shrubland-affiliated species (Ernest et al. 2008); however our results indicate that this reorganization did not occur gradually but through relatively discrete events roughly every 10-15 years (Fig. 1). These rapid changes seem to be the primary dynamic explaining the shift at the site from a rodent community dominated by large-bodied grassland-affiliated species to a smaller-bodied shrubland-affiliated assemblage.

Given the shift in the assemblage from grassland- to shrubland-affiliated species, the primary driver of the change in our rodent community is most likely the increase in shrubs at the site. While we do not have high-frequency observations of this habitat change, shrub growth dynamics are known to be slow compared to the rapid change we observed in the rodent community (Goslee et al. 2003). While the rodent community did, in a broad sense, track this environmental change, it seems unlikely that changes in the rodent community occurred in sync with changes in habitat. The step-wise changes in the rodent community suggest that shifts in which niche traits are favored by the environment as habitat shifts is only part of the story.

When we examine the timing of the rapid transitions, there is a coincidence between the location of the change-point distributions and low abundance periods for the rodents (Fig. 2). Not all low abundance events are associated with rapid shifts in composition, but all rapid transitions in composition are associated with low abundance events. The abundance of an entire community can drop for a variety of reasons (e.g., low resource availability, disturbances, disease, or predation events) and we do not have the data to examine all possibilities. However, some indirect evidence suggests that low resources and disturbances may be contributing to the occurrence of low abundance events in our system. As in many ecosystems, our ecosystem experiences both periodic droughts and extreme rainfall events. Droughts reduce resource availability in this water-limited system, and extreme rainfall events can cause sheet flooding (Thibault and Brown 2008) or saturate soils and damage food stores for granivorous rodents (Valone et al. 1995). All four of our detected change-points, including the longer transition in the 1990s, overlap or occur adjacent to droughts or high rainfall events: 1) an intense tropical storm in October 1983 (Valone et al. 1995), 2) a drought in the 1990s (Allington et al. 2013; Appendix S2: Fig. S6), 3) a sheet flood during monsoon season in August 1999 (Thibault and Brown

2008), and 4) a period of low plant productivity in 2009 (Appendix S2: Fig. S6). However, it is important to note that not all droughts and high rainfall events in this system are associated with low abundance events. For example, low plant productivity also occurred in 2003 (Appendix S2: Fig. S6), but neither abnormally low abundances nor a transition in community composition occurred during that time. If climate events are driving low abundance and rapid ecological transitions, then their impact on the rodent community must also depend on other factors that mitigate those effects.

Regardless of the drivers, there are a variety of processes that could cause a community experiencing low abundance to have an increased likelihood of a rapid ecological transition. Low abundances may occur because the dominant species has been hit disproportionately hard – as happened in our 1983 transition event when the dominant species *D. spectabilis* experienced a population crash (Valone et al. 1995). Removing or reducing dominant species can restructure communities (e.g. Sasaki and Lauenroth 2011) by providing niche opportunities to other species (Shea and Chesson 2002). Alternatively, events that reduce all species to low abundance may increase the role of stochasticity in determining competitive outcomes and can result in the establishment of alternative community compositions (Orrock and Fletcher 2005). Low community abundance also creates opportunities for colonization. Stochasticity in the order of colonization as a community recovers from low abundance can send community assembly down different trajectories (Fukami et al. 2010). Thus low abundance events may be critical junctures where a variety of forces may operate, either singly or in concert, to drive communities toward new assembly trajectories. The prevalence of stochastic processes when abundances are low may also explain why low abundance events do not always result in sudden ecological transitions – sometimes processes will align to create new compositions, but sometimes they will recreate the previous community structure.

Given that our reorganization events appear to be tracking the shift in environment, it seems unlikely that stochastic processes alone explain why our community structure changes after low abundance events. One possibility is that processes similar to priority effects give an advantage to the previously established community, making reorganization in response to gradual changes in the environment more difficult. Through interference competition, inferior competitors can delay or prevent the colonization of a superior competitor if the inferior species is numerically dominant (Amarasekare 2002, Thibault and Brown 2008). As our environment shifted from grassland to shrubland, species that were competitively dominant in the grassland would have slowly become competitively inferior to species better suited to shrubland. However, through numerical superiority and interference competition (e.g. territoriality and seed caching, in our system), they may have impeded the establishment and growth of more superior competitors. Reductions in abundance would remove this 'incumbent advantage' by creating a clean slate where superior competitors can now dominate a community. While the ability of an established community to resist new colonists is well-documented in the context of invasive species (Corbin and D'Antonio 2004), its role in determining how communities track environmental change has received less attention (but see Thibault and Brown 2008). The 'incumbent advantage' may also explain why low abundance events do not always generate rapid transition events. If low abundances occur under conditions where the numerically dominant species is still competitively dominant, the community should simply reassemble to its pre-disturbance state. Only when there is a mismatch between which species is competitively dominant and which is numerically dominant do we expect rapid transitions after low abundance.

Our results show that long-term community change in our intensively studied rodent community did not occur gradually. Although changes in rodent community composition appear to track changes in the environment at the multi-decadal scale, this community change occurred in discrete jumps. Further study to determine whether long-term change through discrete jumps is a common phenomenon or unique to this system is critical for understanding whether systems that appear stable today may be on the verge of rapid ecological transitions. However, rectifying long-term multidecadal scale changes with the short-term dynamics that create that change requires long-term, high frequency monitoring, emphasizing growing concerns (Hughes et al. 2017) that maintaining long-term studies will be critical for detecting, understanding, and predicting future changes in nature.

Figure 1

Figure 1. a) species composition of the four community-types produced by the LDA model, with species arranged on the x-axes by decreasing body size, and grassland-affiliated species emphasized by black boxes around the bars (see Appendix S2: Table S1); **b)** prevalence of the four community-types over time as estimated by the LDA model; **c)** histograms of four change-points representing the greatest changes in the prevalence of community-types from b; and **d)** the change-point model's estimate of how community-type prevalence changes before and after each transition point. Species codes in panel a: NA = *Neotoma albigula*, DS = *Dipodomys spectabilis*, SH = *Sigmodon hispidus*, SF = *Sigmodon fulviventer*, SO = *Sigmodon ochrognathus*, DO = *Dipodomys ordii*, DM = *Dipodomys merriami*, PB = *Chaetodipus baileyi*, PH = *Chaetodipus hispidus*, OL = *Onychomys leucogaster*, OT = *Onychomys torridus*, PL = *Peromyscus leucopus*, PM = *Peromyscus maniculatus*, PE = *Peromyscus eremicus*, PP = *Chaetodipus penicillatus*, PI = *Chaetodipus intermedius*, RF = *Reithrodontomys fulvescens*, RM = *Reithrodontomys megalotis*, RO = *Reithrodontomys montanus*, BA = *Baiomys taylori*, PF = *Perognathus flavus*.

Figure 2

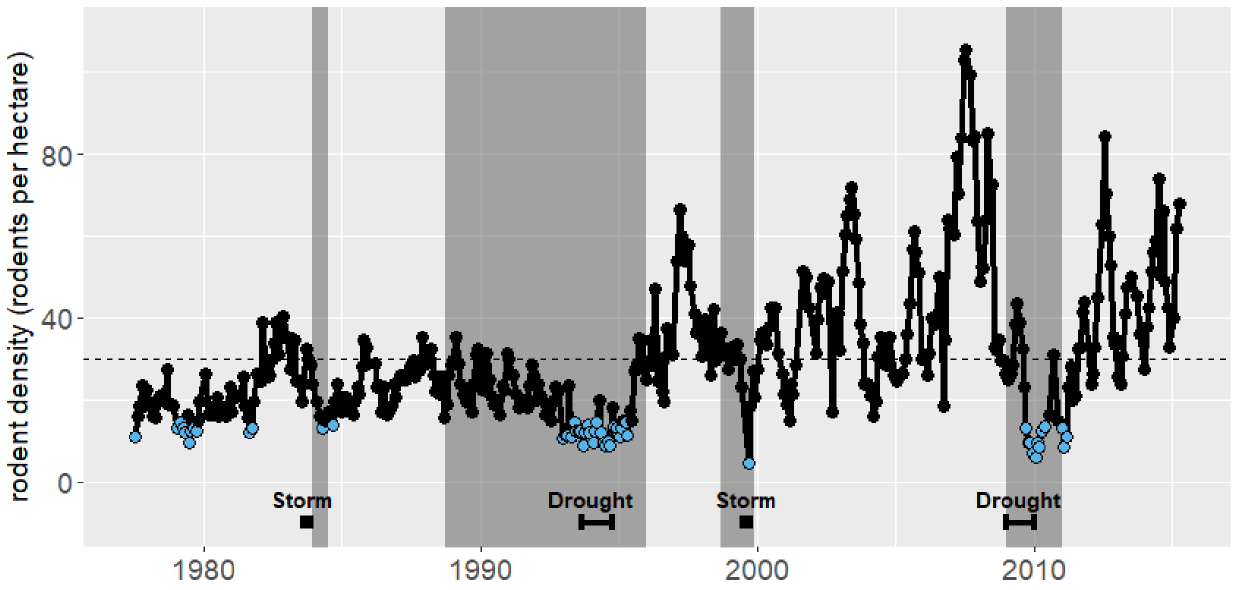

Figure 2. Total rodent abundance per hectare over time. Horizontal dotted line shows long-term mean. Grey vertical bars show the 95% confidence interval for each of the community transition events. Light blue dots are data points in the 0.15 quantile of the negative binomial distribution fit to the data. Locations in time of the two droughts and two storm disturbance events are shown.

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Appendix S1: Supplementary explanation of methods, and demonstration using a simulated data set

LDA is easiest to understand as a generative model, moving from the top of Figure S1 to the bottom. LDA postulates that species assemblages are composed of random samples from a relatively small number of community-types, which are defined in terms of relative species composition (Fig. S1A). In this context, community-types (referred to as “topics” in most of the LDA literature), could represent guilds, clades, or other groups of species whose abundances tend to rise and fall together. Assemblages (Fig. S1C) are generated by randomly drawing species from each of these community-types, with the relative frequency of each community-type determined by the proportions in Fig. S1B.

Fitting an LDA model thus involves simultaneously determining two sets of numbers: one defining the community-types (Fig. S1A), and one describing the observed species assemblages in terms of those types (Fig. S1B). This requires working backwards from observed patterns to infer the parameters of a possible underlying process – i.e., moving in Figure 3 from panel D up to panels A and B

We simulated the simple scenario of two community-types containing overlapping sets of species, but with different permutations of species’ relative abundances (Fig. S2a). Using these two community-types, we simulated three types of dynamics: 1) a fast transition from one community-type to the other (Fig. S2b), 2) a slow transition (Fig. S2c), and 3) constant proportions of the two community-types over time (Fig. S2d). Applied to the simulated data, the LDA model reproduced the composition of the two simulated community-types (Fig. S2e,f) and the dynamics of the fast and slow change scenarios (Fig. S2h,i). The model failed to reproduce the simulated data when the two community-types were represented by constant proportions over time (Fig. S2g,j). This illustrates a limitation of the LDA approach: if there is no change in dominance from one community-type to another (i.e. “stable” community configuration over time), the algorithm will have difficulty distinguishing the two community-types.

When change is fast, the change point model identifies a narrow range of times as the likely location of the shift from one community type to another (Fig. S2k). When change is slow, it is less certain where this shift occurs and the distribution of change-point locations is wider (Fig. S2l). A uniform distribution emerged when no change occurred (Fig. S2m).

Figure S1. Graphical representation of the LDA model. **A.** Community-type definitions: the relative species composition of each community-type; **B.** Community-type proportions: the relative frequency of each community-type contributing to assemblages; **C.** Assemblages: generated by randomly drawing species from the community-type pools in A according to the proportions in B; **D.** Species composition of assemblages, as would be seen in actual community data.

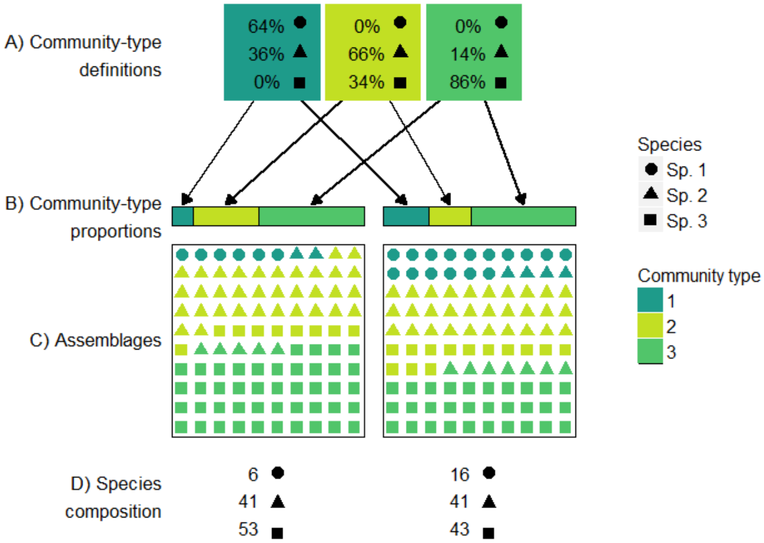
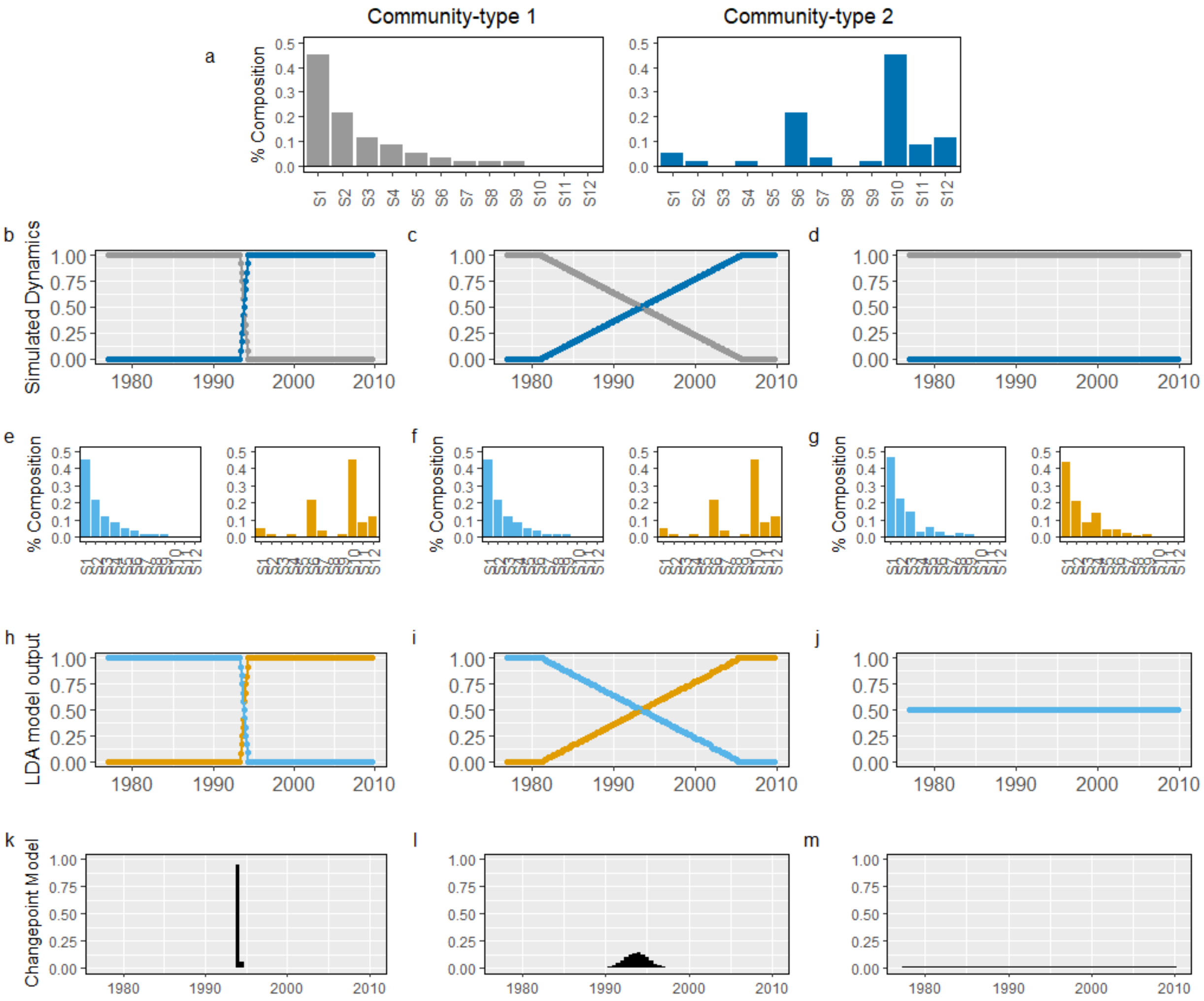


Figure S2. Demonstrating LDA and change-point model using simulated data. **a)** species composition of two community-types to be simulated; **b)** simulation of rapid transition from community-type 1 to community-type 2; **c)** simulation of gradual transition from community-type 1 to community-type 2; **d)** simulation of unchanging community dynamics; **e-g)** species composition of two community-types as output from the LDA model; **h-j)** output of LDA model, trying to recover dynamics simulated in panel b-d; **k-m)** histograms showing the distribution of estimated change-point location.



Appendix S2: supplemental figures and tables

Table S1. Species relative abundances in four community-types estimated by LDA model
Figure S1. Histogram of “best” number of community-types as estimated using 200 random seeds
Figure S2. Comparison of change-point models fit with 2, 3, 4, or 5 change-points.
Figure S3. Results of LDA model fit with three community-types
Figure S4. Results of LDA model fit with four community-types
Figure S5. Results of LDA model fit with five community-types
Figure S6. Normalized Difference Vegetation Index (NDVI) yearly average for 1984-2015.

Table S1: species relative abundances in the four community-types estimated by the LDA model. Species codes: NA = *Neotoma albigula*, DS = *Dipodomys spectabilis*, SH = *Sigmodon hispidus*, SF = *Sigmodon fulviventer*, SO = *Sigmodon ochrognathus*, DO = *Dipodomys ordii*, DM = *Dipodomys merriami*, PB = *Chaetodipus baileyi*, PH = *Chaetodipus hispidus*, OL = *Onychomys leucogaster*, OT = *Onychomys torridus*, PL = *Peromyscus leucopus*, PM = *Peromyscus maniculatus*, PE = *Peromyscus eremicus*, PP = *Chaetodipus penicillatus*, PI = *Chaetodipus intermedius*, RF = *Reithrodontomys fulvescens*, RM = *Reithrodontomys megalotis*, RO = *Reithrodontomys montanus*, BA = *Baiomys taylori*, PF = *Perognathus flavus.*

	Community-type 1	Community-type 2	Community-type 3	Community-type 4
NA	0.088	0.025	0.024	0.001
DS	0.340	0.000	0.000	0.000
SH	0.001	0.004	0.020	0.000
SF	0.000	0.003	0.014	0.000
SO	0.000	0.001	0.000	0.000
DO	0.076	0.128	0.211	0.018
DM	0.341	0.606	0.078	0.216
PB	0.000	0.000	0.450	0.025
PH	0.000	0.001	0.000	0.000
OL	0.061	0.030	0.003	0.001
OT	0.051	0.064	0.130	0.006
PL	0.000	0.000	0.004	0.000
PM	0.000	0.012	0.006	0.000
PE	0.011	0.041	0.016	0.000
PP	0.000	0.000	0.022	0.722
PI	0.000	0.000	0.006	0.002
RF	0.000	0.001	0.000	0.000
RM	0.000	0.049	0.000	0.000
RO	0.000	0.001	0.000	0.000
BA	0.000	0.001	0.009	0.002
PF	0.030	0.032	0.007	0.006

Figure S1. We estimated model fit using an approximate AIC procedure for LDA models using 2 to 9 community-types. Since LDA depends on a random seed, we repeated the LDA model fit and AIC model selection using 200 different seeds to obtain a distribution of "best number of community-types." This procedure always selected between 3 and 5 community-types, with 4 selected by the majority of runs.

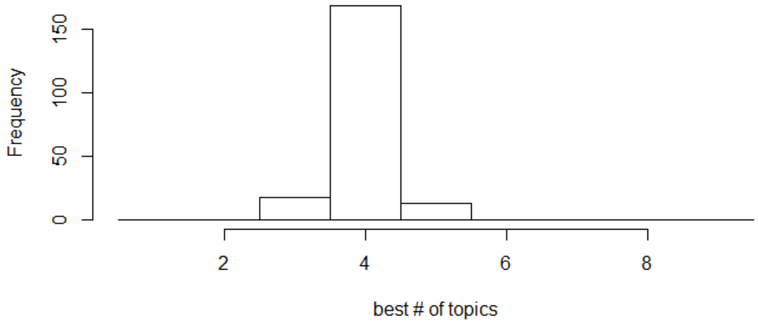


Figure S2. Comparison of change-point models fit with 2, 3, 4, or 5 change-points. The model containing 4 change-points was best supported.

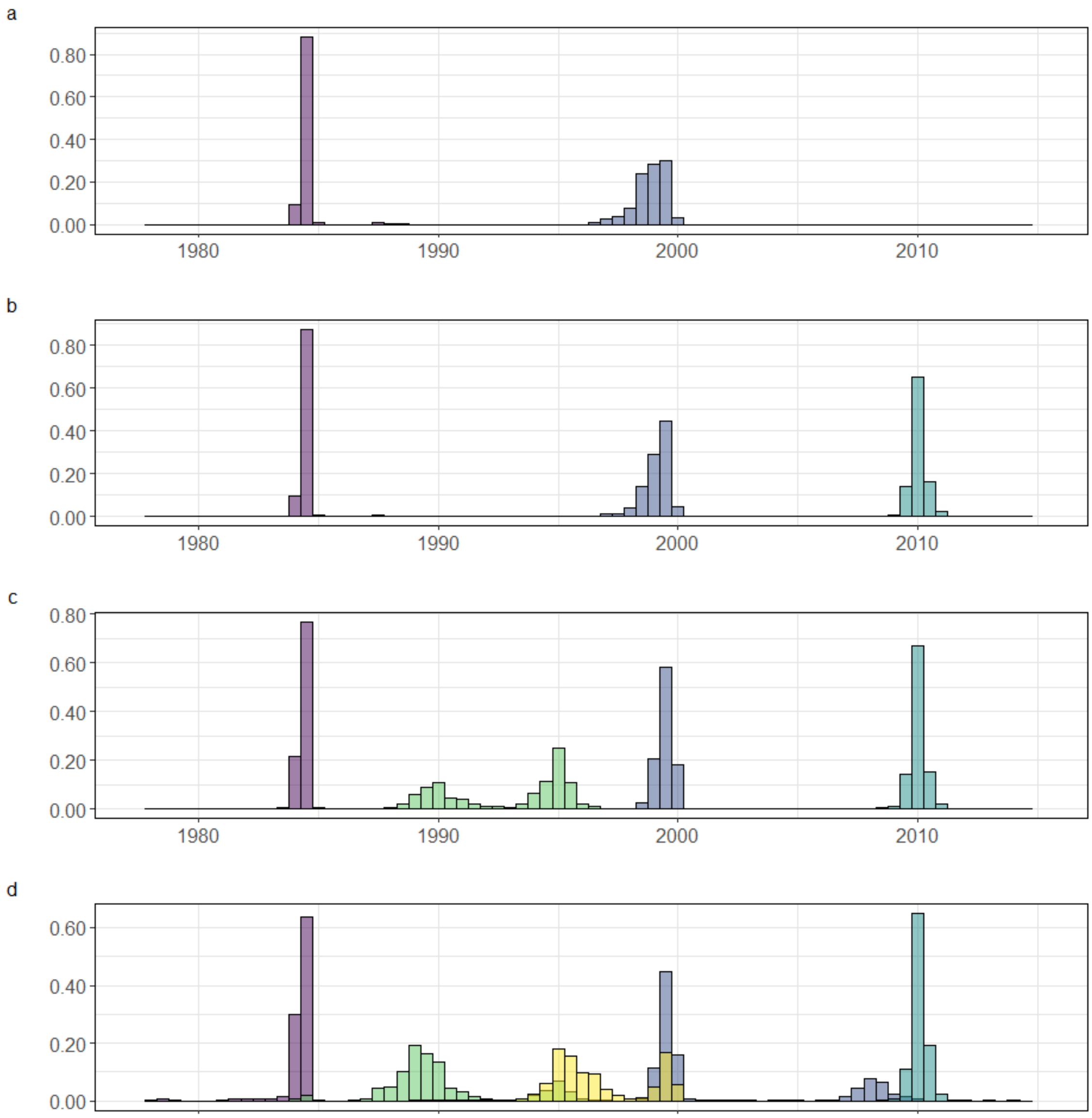


Figure S3. Results of LDA model fit with three community-types

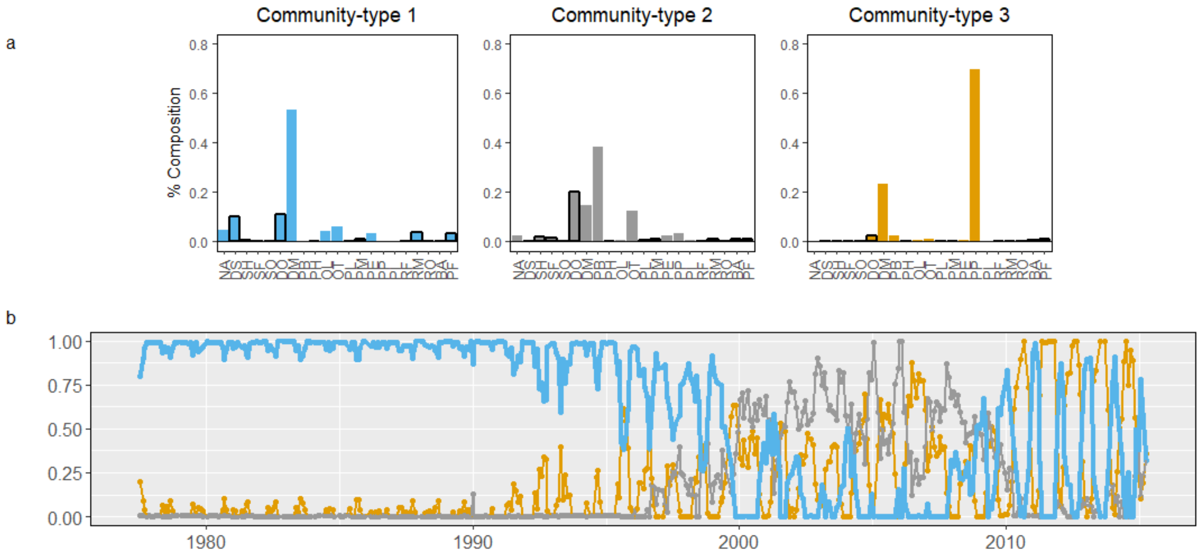


Figure S4. Results of LDA model fit with four community-types

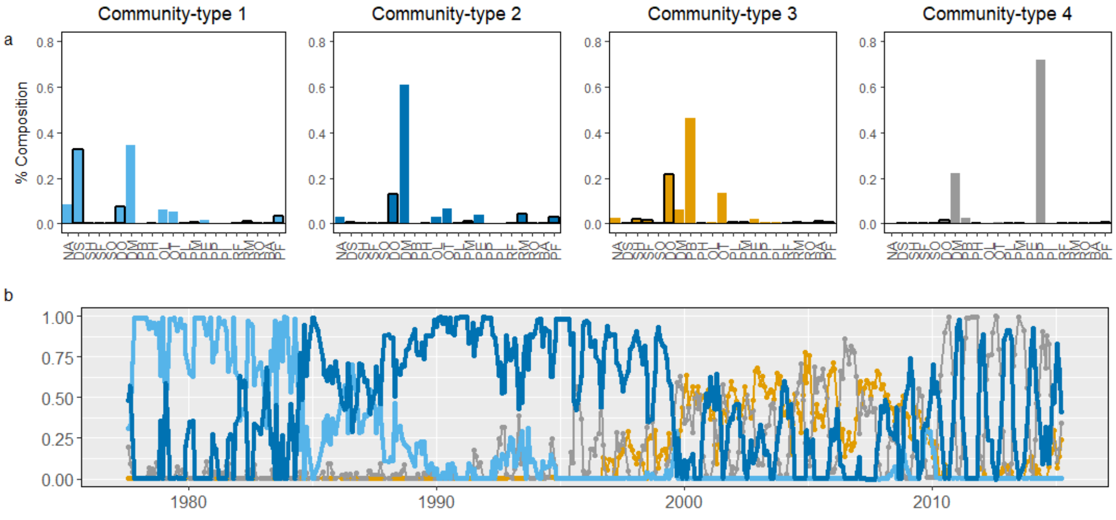


Figure S5. Results of LDA model fit with five community-types

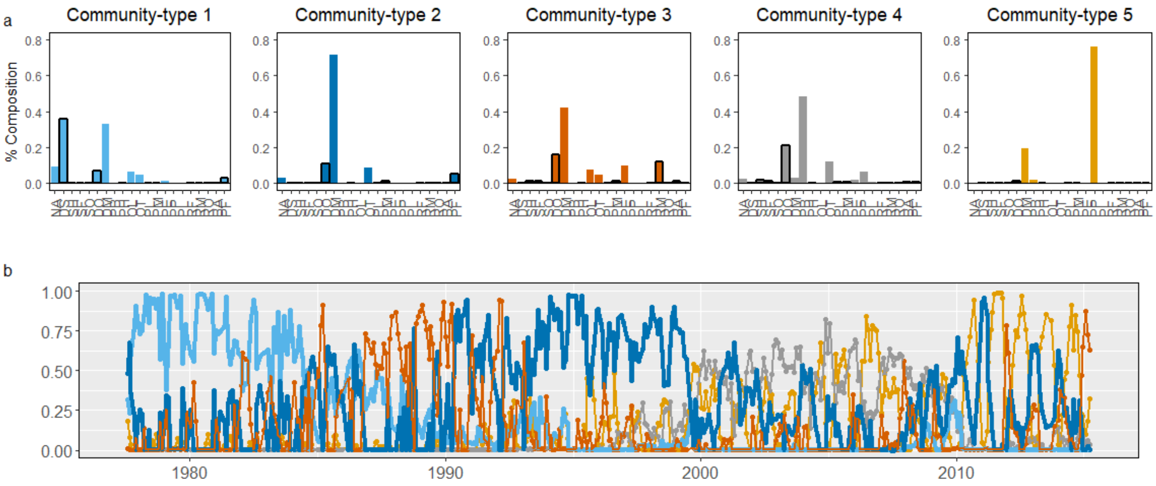


Figure S6. Normalized Difference Vegetation Index (NDVI) yearly average for 1984-2015. NDVI values were obtained from a combination of data from satellites Landsat 4, 5, 7, and 8. Raster NDVI files were downloaded from earthexplorer.usgs.gov and clipped to a 5 km^2 area centered over the Portal Project site. We calculated median NDVI value for each 5 km^2 image, and calculated correction factors based on the periods of overlap between satellites so data from all satellites could be directly compared. We calculated a time series of average yearly NDVI for each year for which there were at least 12 images spanning at least 6 months of the year.